

DESCRIPTION OF THE RADULA OF *BUCCINANOPS GLOBULOSUS* (NEOGASTROPODA, NASSARIIDAE) AND AN ASSESSMENT OF ITS VARIABILITY IN NORTHERN PATAGONIAN GULFS

María S. Avaca^{1, 2*}, Maite Narvarte^{1, 3} & Pablo R. Martín^{1, 4}

INTRODUCTION

Buccinanops globulosus (Kiener, 1834) is an endemic macrofaunal component of coastal waters of the southwestern Atlantic Ocean (34°–48°S). This species inhabits sandy or muddy patches in the low intertidal zone to 10 m depth, where it spends most of the time buried (Scarabino, 1977). Its diet is mainly composed by carcasses of dead crabs, *Cyrtograpsus angulatus* and *Neohelice granulata* (Daleo et al., 2005), or the clam *Amiantis purpurata* (Narvarte, 2006). It has a great capacity to detect and rapidly consume carrion, generally outcompeting other scavengers (Daleo et al., 2005).

This species shows great interpopulation variability in many life history traits, including growth rate, size and age at first maturity, and fecundity (Narvarte et al., 2008). Such variation has been attributed to the effect of different environmental conditions, such as food availability, thus being an expression of phenotypic plasticity. Development is direct; crawling juveniles emerge and live in the same area as adults, thus restricting dispersal capability (Penchaszadeh, 1971). Owing to this reproductive strategy and the reduced mobility of adults, *B. globulosus*, as other species of gastropods with similar life history, may form isolated enclaves and may adapt to local conditions (Johannesson & Johannesson, 1993; Johannesson et al., 1993; Rochette et al., 2003; Sokolova & Boulding, 2004).

The radula is the major feeding organ of most gastropods, its structure related to diets and feeding modes. Radular characteristics have been employed for taxonomic purposes, being considered specific to species (Fretter & Graham, 1984), and at the generic and supra-generic levels (Reid, 1996; Nishi & Kohn, 1999; Franklin et al., 2007). However, intraspecific

variation has also been reported and linked to differences in diet, food availability or habitat, and between ontogenetic stages, sexes, or populations (Nybakken, 1990; Padilla, 1998; Maintenon, 2004; Onitsuka et al., 2004; Andrade & Solferini, 2006).

The radula has been described for only two out of the five to seven species currently recognized in the genus *Buccinanops* (Pastorino, 1993; Simone, 1996), and little is known about its intraspecific variability. In this work, we describe the radula of *B. globulosus* and assess its variability among and within three populations in northern Patagonia. Populations selected for this study differ in maximum size, growth rate, size and age at first maturity, and fecundity (Narvarte et al., 2008; Avaca et al., 2009). Taking into account these differences and their possible relationship with environmental conditions at each site, it is interesting to discern if those differences also include radular characteristics.

MATERIAL AND METHODS

Sampling sites were located in the north Patagonian gulfs San Matías (SMG, two sampling sites: Villarino Beach and San Antonio Bay) and Nuevo (NG, one sampling site: Nueva Bay) (Fig. 1).

San Matías Gulf is the largest north Patagonian gulf, with a surface area of approximately 20,000 km², while Nuevo Gulf is relatively small, having only 2,400 km² (Rivas, 1990). Villarino Beach (40°45'S, 64°30'W) is an exposed beach located in northern SMG. Tides have a semidiurnal regime, with mean and maximum amplitudes of 6.32 m and 8.76 m, respectively. The slope of the beach is slight, and at low tides a large area of tidal flats, approximately 450–

¹Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)

²Instituto de Biología Marina y Pesquera Almirante Storni, Av. Güemes 1030, 8520 San Antonio Oeste, Río Negro, Argentina

³Instituto Multidisciplinario de Investigación y Desarrollo de la Patagonia Norte (IDEPA), San Martín 247, 8520 San Antonio Oeste, Argentina

⁴Laboratorio de Ecología, Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, San Juan 670, 8000 Bahía Blanca, Argentina

*Corresponding author: msavaca@yahoo.com.ar



FIG. 1. Map showing sampling sites for *Buccinanops globulosus*; Villarino Beach (1), San Antonio Bay (2) and Nueva Bay (3).

600 m wide, is exposed (Morsan, 2003). The bottom is composed mainly of fine sand. At this site, *B. globulosus* occupies the intertidal and subtidal zone where the purple clam, *Amiantis purpurata*, is the main macrofaunal component (Morsan & Orensanz, 2004). San Antonio Bay ($40^{\circ}45'S$, $64^{\circ}56'W$) is a salt marsh located in a semiclosed area in the northwest coast of SMG (Schnack et al., 1996). It has a semidiurnal tidal pattern, with a range variable from 6 m to 9 m and a maximum depth of 4 m at low tide. This area is highly influenced by local atmospheric conditions (Rivas, 1990, 1994). Small pebbles alternating with sand flats and large beds of the mussel *Brachydontes rodriguezii* constitute the main substrata.

Nueva Bay ($42^{\circ}45'S$, $65^{\circ}02'W$) is located in the west of Nuevo Gulf near Puerto Madryn, one of the most urbanized coastal sites of Argentine Patagonia. Tides have a semidiurnal regime, with mean and maximum amplitudes of 3.66 m and 5.47 m, respectively. The slope of the beach is low, with an extensive intertidal zone of approximately 250 m wide. The bottom is formed by coarse sediments, mostly sand with sparse gravel and shell fragments, with outcrops of base rocks in some places (Solís, 1998).

Specimens of *B. globulosus* were collected during a two-year period (2006–2008). At diurnal tides, fish baits were employed to attract whelks during both low and high tides. Although whelks rapidly emerge from the sediment in

response to food stimuli, bait was left for 20 min in order to ensure the attraction of individuals of all size classes present. Attracted whelks were collected (by snorkeling during high tides) and carried in plastic bags filled with sea water to the laboratory.

Once in laboratory, whelks were frozen in order to facilitate the dissection of radulae. Total shell length (TSL, parallel to the columelar axis) was measured using Vernier calipers (± 0.01 mm). Due to the occurrence of imposex in two of the studied populations, San Antonio Bay and Nueva Bay (Bigatti et al., 2009; Nudelman et al., in press), sex was determined on the basis of the presence of an albumen gland in females and by its absence and the presence of a penis in males.

Each individual was dissected when defrosted, and its radula was removed from the proboscis. Radulae were cleaned in 5% sodium hypochlorite in distilled water for 10 min, dried at 25°C and mounted in water on glass slides. The number of rows (NRO) per ribbon, the number of rachidian (NRC) and lateral cusps on each radula (NLC) were counted under a Nikon stereoscopic microscope. Total length of the radula ribbon (TRL) and the height of central rachidian cusp (HCC) of at least ten individuals per site were measured using a micrometric eyepiece.

Voucher specimens (mounted radulae) have been deposited in Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (MACN) under the following collection numbers 37889, 37890 and 37891.

Scanning electron microscope (SEM) observations were made on four individuals from Villarino Beach and on three from the other two populations. For this purpose, 5 mm-long

portions, were critical-point dried, mounted on stubs, gold coated, and observed with an EVO 40 SEM operated at accelerating voltage of 7 KV.

The description of the radula characters was based on Pastorino (1993) and Simone (1996); in our study, the central tooth is referred to as the rachidian tooth and cusps present in lateral teeth as inner, outer and middle. The counting of cusps was restricted to one row of the central part of the radula ribbon in order to avoid counting them on teeth worn or in a replacement process. The number of cusps on lateral teeth was recorded only from the right margin of each radula.

To test the relationship between TSL and morphometric variables of radula (TRL, NRO, NRC, HCC, NMC), Spearman’s rank correlation analyses (Sokal & Rohlf, 1995) were performed for the pooled data and separately for each population. Differences among populations for all the radula variables were assessed using a non-parametric Kruskal-Wallis variance analysis, while intersex differences for the same set of variables were assessed by U test (Sokal & Rohlf, 1995). The α level of these tests was adjusted by Bonferroni correction.

Comparisons between sexes were assessed only with mature females and males, which were considered so if larger than the size at first maturity for females of each population (i.e., minimum shell length of a female carrying egg capsules: 14.5, 22.1 and 45.0 mm for San Antonio Bay, Nueva Bay, and Villarino Beach, respectively (Narvarte et al., 2008; Avaca et al., 2009). Owing to the intersexual differences in growth rate, male maturity may be attained at a smaller size than that of females, but no other external criterion of male maturity was available.

TABLE 1. Descriptive statistics for total shell length (TSL, mean $\pm$ standard deviation), number of rows (NRO, median), number of rachidian (NRC, median) and middle cusps (NMC, median) for the studied populations.

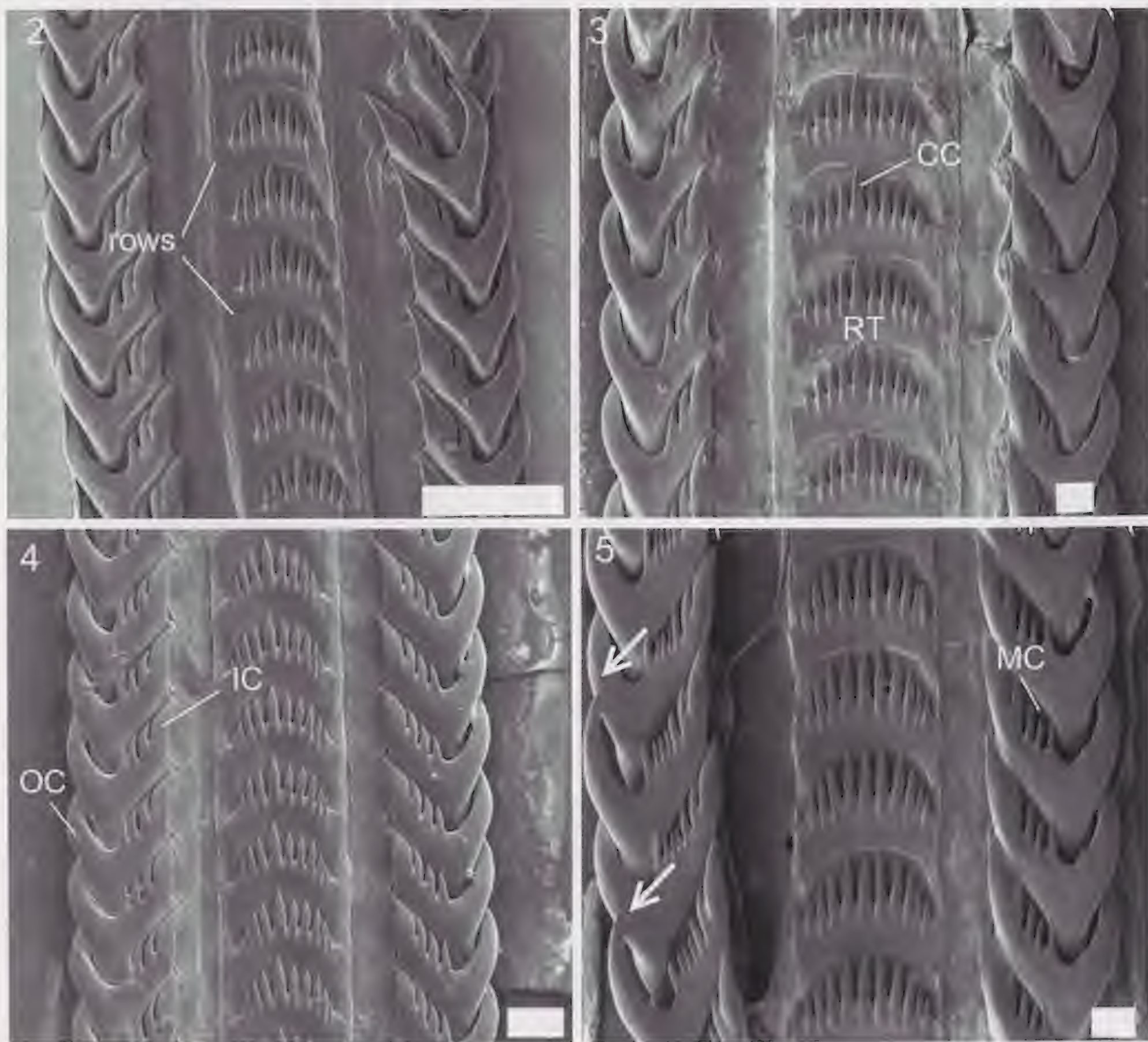
Population	TSL	NRO	NRC	NMC
San Antonio Bay	16.03 $\pm$ 3.54 (n = 77)	61	8	2
Range	8.35–24.82	37–77	6–10	1–3
Villarino Beach	35.65 $\pm$ 12.87 (n = 76)	70	9	2
Range	14.37–62.51	62–87	6–12	2–4
Nueva Bay	27.3 $\pm$ 8.7 (n = 81)	70.5	8	2
Range	13.47–46.77	54–83	6–10	2–4

RESULTS

Buccinanops globulosus has a rachiglossan radula, the number of transverse rows per ribbon varying between 37 and 87. The rachidian tooth was multicuspitate, with 6 to 12 well-spaced cusps that decrease in size from the central cusp outwards (Figs. 2–5). Generally, the number of cusps was the same to both sides of the central rachidian cusp. The rachidian teeth base was slightly concave. The lateral teeth have an inner cusp (sometimes bifid), 2–3 middle cusps and an outer cusp. The inner

and outer cusps are curved towards rachidian tooth, the outer cusp being the largest. Differences in the number of middle cusps between right and left side were observed (Fig. 5). No differences in teeth shape among populations were observed.

Specimens of *B. globulosus* varied markedly in size among populations (Kruskal - Wallis H ($df = 2$) = 114.01, $p < 0.001$, Table 1). Positive significant relationships between TSL and total radula length (TRL), number of rows (NRO), number of rachidian (NRC) and middle cusps (MMC), and central cusp height (HCC) were

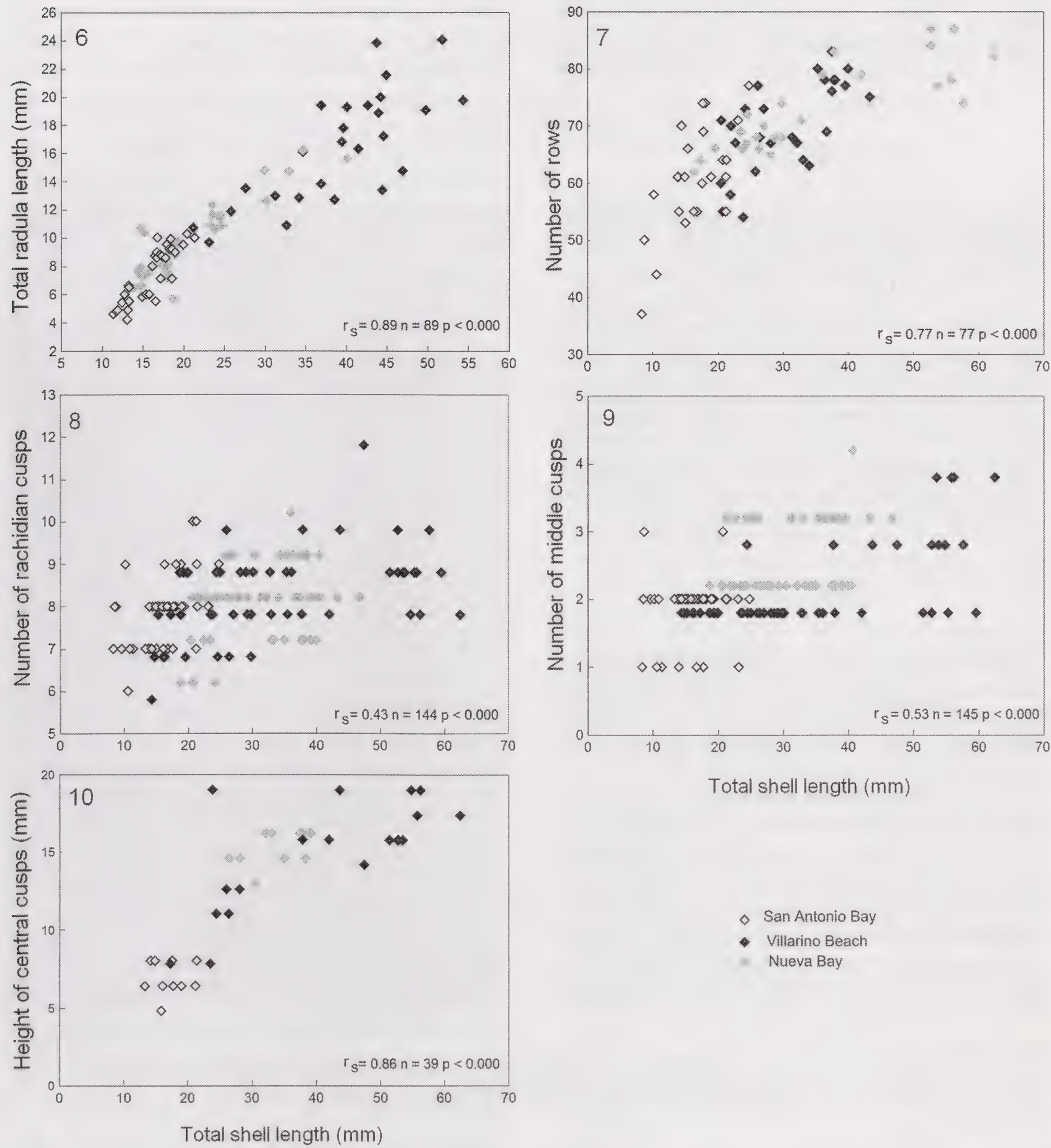


FIGS. 2–5. Scanning electron micrographs (SEM) of radular teeth of *Buccinanops globulosus*. FIG. 2: Radula from San Antonio Bay, 8 rachidian cusps, 2 middle cusps; FIG. 3: Radula from Villarino Beach, 10 rachidian cusps, 3 middle cusps; FIG. 4: Radula from Nueva Bay, 10 rachidian cusps, 3 middle cusps; FIG. 5: Radula of an individual from Villarino Beach showing 5 middle cusps, bifid inner lateral cusps and the fusion of 2 lateral outer cusps (arrows). Scale bars: FIG. 2 = 200 μm ; FIGS. 3–5 = 100 μm . CC = central cusp, IC = inner cusp, MD = middle cups, OC = outer cusp, RT = rachidian teeth.

found when the three populations were analyzed together (α global < 0.05) (Figs. 6–10); a steepest increase in the number of rows and in the length of the radula and central cusps was apparent for smaller whelks. Most of these relationships were also found to be significant within each population (Table 2); all the mor-

phometrics variables of radula were positively and significantly correlated with shell size at Villarino Beach.

Intrapopulation variability was observed both in the number of rachidian cusps and in the number of middle cusps (Table 1). No sexual dimorphism was found in the radular variables,



FIGS. 6–10. Bivariate scatterplots for total shell length *versus* radular variables of *Buccinanops globulosus* in the studied populations. FIG. 6: Radula total length; FIG. 7: Number of rows per ribbon; FIG. 8: Number of rachidian cusps; FIG. 9: Number of middle cusps; FIG. 10: Height of central rachidian cusps. r_s : Spearman's rank correlation coefficient. In order to facilitate visualization ± 0.2 were added to the data of number of cusps for Nueva Bay and Villarino Beach, respectively.

TABLE 2. Summary of non parametric Spearman’s rank correlation tests between total shell length and radula morphometric variables within each studied population. HCC: height of central rachidian cusps, NMC: number of middle cusps, NRC: number rachidian cusps, NRO: number of rows, TLR: total radula length, r_s : Spearman’s rank correlation coefficient. **: $p < 0.001$, *: $p < 0.05$, ns: $p > 0.05$.

Population	TLR	NRO	NRC	NMC	HCC
San Antonio Bay	$r_s = 0.87^{**}$ n = 32	$r_s = 0.60^{**}$ n = 24	$r_s = 0.51^{**}$ n = 45	$r_s = 0.49$ ns n = 45	$r_s = 0.05$ ns n = 10
Villarino Beach	$r_s = 0.75^{**}$ n = 26	$r_s = 0.86^{**}$ n = 26	$r_s = 0.45^*$ n= 49	$r_s = 0.59^{**}$ n = 50	$r_s = 0.66^{**}$ n = 19
Nueva Bay	$r_s = 0.85^{**}$ n = 31	$r_s = 0.68^{**}$ n = 27	$r_s = 0.26$ ns n = 50	$r_s = 0.32^*$ n = 50	$r_s = 0.47$ ns n = 10

neither when pooling males and females from the three populations (NRO: $H (df = 1) = 2.73$, $p = 0.08$, $n = 46$; NRC: $H (df = 1) = 0.41$, $p = 0.52$, $n = 85$; NMC: $H (df = 1) = 2.38$, $p = 0.12$, $n = 85$ nor when comparing males and females within each population (U test $p > 0.05$ for each population and variable). Shell size differences were found between sexes within each studied population (U test, $p < 0.001$); intersexual comparisons could not be made within Villarino Beach population because only one mature male was contained in the sample.

DISCUSSION

The radula of *B. globulosus* has a morphological pattern similar to that of other species of *Buccinanops*, *B. cochlidium* and *B. moniliferus* (Pastorino, 1993; Simone, 1996; Table 3). This species has a rachiglossan radula with 6–12 rachidian cusps per row and lateral teeth with inner, middle and outer cusps. This type of radula is characteristic of non-active predators or scavengers (Castellanos, 1967). However, we have observed whelks inserting their proboscis between the open valves of healthy individuals of the purple clam, *Amiantis purpurata*, at one of the study sites (Villarino Beach), thus indicating

that *B. globulosus* may also feed on live organisms. This is not surprising, because almost all predators are also facultative scavengers and vice versa (Kaiser et al., 2005).

The variation observed in the number of cusps (rachidian and laterals) and in height of central rachidian cusps among and within populations of *B. globulosus* do not involves the general radular morphology. These differences appear to be size related, as shown by the positive relationships found between these variables and total shell length. Several authors have reported increasing values in radula morphometric variables, such as length, width, and number of tooth rows with increasing total length, for instance in *Haliotis rubra* (Johnston et al., 2005) and in several muricids (Harding et al., 2008; Fujioka, 1985; Kool, 1993). However, despite size differences between sexes (Narvarte et al., 2008; this study), no sex-related differences were found in the radular variables. Similar results were found by Pastorino (1993) for the radula of *B. cochlidium*, while Simone (1996), despite noteworthy intersexual differences in size, did not mention radular differences between sexes in *B. moniliferus*.

Our findings suggest that feeding behavior of *B. globulosus* is similar across populations and that it remains constant during most of its

TABLE 3. Radular characters in *Buccinanops* species. NMC: number of middle cusps, NRC: number of rachidian cusps, TSL: total shell length (mm).

Species	TSL	NRC	NMC	References
<i>B. moniliferus</i>	up to 50	9–11	1–4	Pastorino, 1993
<i>B. cochlidium</i>	15.4–91.00	5–11	1–3	Simone, 1996; Pastorino, 1993
<i>B. globulosus</i>	8.35–62.51	6–12	1–4	This work

ontogeny. Field observations confirm that individuals of both sexes from a wide size range may feed on the same carcasses. Also a high degree of gregariousness in feeding activity, more than 30 individuals per carcass, was observed. This is common among scavengers, because carrion availability is ephemeral and unpredictable (Daleo et al., 2005), but it usually occurs in large amounts. For the smaller whelks studied, the variables related to the size of the radula and its teeth change faster relative to shell size than other size classes, suggesting a rapid growth of the radular system and proboscis. Perhaps this is related to the ontogenetic dietary changes (from detritivory to scavenging and predation) that have been reported for other nassariids (Tallmark, 1980). The newborn of *B. globulosus* do not feed on fish meat under laboratory conditions (pers. obs.).

Morphometric radular differences among the studied populations are clearly related to their variation in size. Differential growth rates observed in *B. globulosus* may be influenced by many factors, including food availability, presence of predators, and temperature. However, it seems that factors promoting size differences are not expressed in radula morphology. Narvarte et al. (2008) suggested that the high food availability observed at Villarino Beach and the low subtidal location of this population may explain the maximum sizes. At this site, the largest bed of the clam *Amiantis purpurata* along its entire distribution is found (Morsan, 2000). This bed could be acting as a carrion source for *B. globulosus* in two ways: directly by supplying of dead individuals and, indirectly, by carrion made by such predators as the crabs *Libinia spinosa* and *Ovalipes trimaculatus* and the gastropod *Odontocymbiola magellanica*, which feed on *A. purpurata* (Morsan, 2000; Narvarte et al., 2007). It is known that the availability of carrion for scavengers may be a limiting factor of growth, reproduction and eventually population size (Rochette et al., 1995; Morton & Chan, 1999; Rochette et al., 2001). Saunders et al. (2009) found that stunted and non-stunted populations of *Haliotis rubra* result mainly from a different food supply between sites.

We conclude that *B. globulosus* is homogeneous for radula characteristics; only size related differences were found among populations. This interpopulation uniformity in the radula supports the idea that the studied populations, despite the great variation in life history traits, would not represent different species, a possibility suggested in a previous work (Narvarte et al., 2008).

ACKNOWLEDGMENTS

Special thanks are due to Kelo Camarero, Andrea Amestoy and Roxana Soler for their technical assistance; also to two anonymous reviewers for their comments. This work was supported by PID 371 ANPYCT (Agencia Nacional de Promoción Científica y Tecnológica) granted to Dr. Raúl González, Maite Narvarte and Antonio Gagliardini. M.S.A thanks Consejo Nacional de Promoción Científica y Tecnológica (CONICET) for a doctoral fellowship.

LITERATURE CITED

- ANDRADE, S. C. S. & V. N. SOLFERINI, 2006, Transfer experiment suggests environmental effects on the radula of *Littoraria flava* (Gastropoda: Littorinidae). *Journal of Molluscan Studies*, 72: 111–116.
- AVACA, M. S., M. A. NARVARTE & P. R. MARTÍN, 2009, Crecimiento individual del caracol *Buccinanops globulosum* en la Bahía Nueva, Golfo Nuevo. *CD Resúmenes VII Jornadas Nacionales de Ciencias del Mar*, Bahía Blanca: 192.
- BIGATTI, G., M. A. PRIMOST, M. CLEDÓN, A. AVERBUJ, N. THEOBALD, W. GERWINSKI, W. ARNTZ, E. MORRICONI & P. E. PENCHASZADEH, 2009, Biomonitoring of TBT contamination and imposex incidence along 4700 km of Argentinean shoreline (SW Atlantic: From 38S to 54S). *Marine Pollution Bulletin* doi:10.1016/j.marpolbul.2009.
- CASTELLANOS, Z. A. DE, 1967, Catálogo de moluscos marinos bonaerenses. *Anales Comisión Investigaciones Científicas*, 8: 1–365.
- DALEO, P., M. ESCAPA, J. P. ISACCH, P. RIBEIRO & O. IRIBARNE, 2005, Trophic facilitation by the oystercatcher *Haematopus palliatus* Temminck on the scavenger snail *Buccinanops globulosum* Kiener in a Patagonian bay. *Journal of Experimental Marine Biology and Ecology*, 325: 27–34.
- FRANKLIN, J. B., S. A. FERNANDO, B. A. CHALKE & K. S. KRISHNAN, 2007, Radular morphology of *Conus* (Gastropoda: Caenogastropoda: Conidae) from India. *Molluscan Research*, 27(3): 111–122.
- FRETTER, V. & A. GRAHAM, 1984, *British prosobranch molluscs, their functional anatomy and ecology*. Ray Society, London, 820 pp.
- FUJIOKA, Y., 1985, Systematic evaluation of radular characters in Thaidinae (Gastropoda: Muricidae). *Journal of Science of Hiroshima University, Series B, Division 1 (Zoology)*, 31: 235–287.
- HARDING, J. M., S. M. GERA & R. MANN, 2008, Radula morphology in veined rapa whelks, *Rapana venosa* (Valenciennes, 1846) (Gastropoda: Muricidae) from Chesapeake Bay, USA. *The Nautilus*, 122(4): 217–227.
- JOHANNESSON, B. & K. JOHANNESSON, 1993, Population differences in behavior and morphol-

- ogy in the snail *Littorina saxatilis*: phenotypic plasticity or genetic differentiation? *Journal of Zoology*, 240: 475–493.
- JOHANNESSON, K., B. JOHANNESSON & E. ROLÁN-ALVAREZ, 1993, Morphological differentiation and genetic cohesiveness over a microenvironmental gradient in the marine snail, *Littorina saxatilis*. *Evolution*, 47(6): 1770–1787.
- JOHNSTON, D., N. MOLTSCHANIWSKYJ & J. WELLS, 2005, Development of the radula and digestive system of juvenile blacklip abalone (*Haliotis rubra*): potential factors responsible for variable weaning success on artificial diets. *Aquaculture*, 250: 341–350.
- KAISER, M. J., M. J. ATTRILL, S. JENNINGS, D. N. THOMAS, D. K. ABARNES, A. S. BRIERLEY, N. V. C. POLUNIN, D. G. RAFFAELLI & P. J. LE B. WILLIAMS, 2005, *Marine ecology: processes, systems and impacts*. Oxford University Press, 557 pp.
- KOOL, S. P., 1993, The systematic position of the genus *Nucella* (Prosobranchia: Muricidae: Ocenebrinae). *The Nautilus*, 107: 43–57.
- MAINTENON, M., 2004, Sexually dimorphic radular morphology in *Euplica varians* and *E. versicolor*. *Molluscan Research*, 24: 179–185.
- MORSAN, E. M., 2000, Dinámica poblacional y explotación de la almeja púrpura *Amiantis purpurata* (Lamarck 1856) (Bivalvia: Veneridae). *Tesis Doctoral*. Universidad Nacional del Sur, Argentina, 120 pp.
- MORSAN, E. M., 2003, Spatial analysis and abundance estimation of the southernmost population of purple clam *Amiantis purpurata* in Patagonia (Argentina). *Journal of the Marine Biological Association of the United Kingdom*, 83: 1073–1082.
- MORSAN, E. M. & J. M. ORENSANZ, 2004, Age structure and growth in an unusual population of purple clams, *Amiantis purpurata* (Lamarck, 1818) (Bivalvia: Veneridae), from Argentine Patagonia. *Journal of Shellfish Research*, 23: 73–80.
- MORTON, B. & K. CHAN, 1999, Hunger rapidly overrides the risk of predation in the subtidal scavenger *Nassarius siquijorensis* (Gastropoda: Nassariidae): an energy budget and a comparison with the intertidal *Nassarius festivus* in Hong Kong. *Journal Experimental Marine Biology and Ecology*, 240: 213–228.
- NARVARTE, M. A., 2006, Biology and fishery of the whelk *Buccinanops globulosum* (Kiener, 1834) in northern coastal waters of the San Matías Gulf (Patagonia, Argentina). *Fisheries Research*, 77: 131–137.
- NARVARTE, M., R. GONZÁLEZ, P. OSOVNIKAR, M. CAMARERO, L. CURTOLO & M. OCAMPO REINALDO, 2007, Experimental trap fishery for the crabs *Platyxanthus patagonicus* and *Ovalipes trimaculatus* in the San Matías Gulf, Patagonia, Argentina. *Journal of the Marine Biological Association of the United Kingdom*, 87: 1235–1242.
- NARVARTE, M., V. WILLERS, M. S. AVACA & M. E. ECHAVE, 2008, Population structure of the snail *Buccinanops globulosum* (Prosobranchia, Nassariidae) in San Matías Gulf, Patagonia Argentina: isolated enclaves? *Journal of Sea Research*, 60: 144–150.
- NISHI, M. & A. J. KOHN, 1999, Radular teeth of indo-pacific molluscivorous species of *Conus*: a comparative analysis. *Journal of Molluscan Studies*, 65: 483–497.
- NUDELMAN, N., C. RODRÍGUEZ, R. WAISBAUM, M. NARVARTE & V. WILLERS, (in press), Aditivos antiincrustantes en costas argentinas y sus efectos sobre organismos marinos autóctonos, in: R. A. LOPARDO, ed., *El agua en la Argentina: una vista desde la academia*.
- NYBAKKEN, J., 1990, Ontogenetic change in the *Conus* radula, its form, distribution among the radula types, and significance in systematics and ecology. *Malacologia*, 32: 35–54.
- ONITSUKA, T., T. KAWAMURA, S. OHASHI, T. HORII & Y. WATANABE, 2004, Morphological changes in the radula of abalone *Haliotis diversicolor aquatilis* from post-larva to adult. *Journal of Shellfisheries Research*, 312: 43–66.
- PADILLA, D. K., 1998, Inducible phenotypic plasticity of the radula in *Lacuna* (Gastropoda: Littorinidae). *The Veliger*, 41: 201–204.
- PASTORINO, G., 1993, The taxonomic status of *Buccinanops d'Orbigny, 1841* (Gastropoda: Nassariidae). *The Veliger*, 32(2): 160–165.
- PENCHASZADEH, P. E., 1971, Aspectos de la embriogénesis de algunos gasterópodos del género *Buccinanops* d'Orbigny, 1841 (Gastropoda, Prosobranchiata, Buccinidae). *Physis*, 30: 475–482.
- REID, D. G., 1996, Systematics and evolution of *Littorina*. Ray Society, London, 228 pp.
- RIVAS, A. L., 1990, Heat balance and annual variation of mean temperature in the north Patagonian gulfs. *Oceanological Acta*, 13: 265–272.
- RIVAS, A. L., 1994, Spatial variation of the annual cycle in the Patagonian shelf between 40 and 50° of south latitude. *Continental Shelf Research*, 14: 1539–1554.
- ROCHETTE, R., F. TÉTREAU & J. H. HIMMELMAN, 2001, Aggregation of whelks, *Buccinum undatum*, near feeding predators: the role of reproductive requirements. *Animal Behavior*, 61: 31–41.
- ROCHETTE, R., K. DUNMALL, L. M. DILL, 2003, The effect of life-history variation on the population size structure of a rocky intertidal snail (*Littorina sitkana*). *Journal of Sea Research*, 49: 119–132.
- ROCHETTE, R., S. MORISSETE & J. H. HIMMELMAN, 1995, A flexible response to a major predator provides the whelk *Buccinum undatum* L. with nutritional gains. *Journal of Experimental Marine Biology and Ecology*, 185: 167–180.
- SAUNDERS, T., S. D. CONNELL & S. MAYFIELD, 2009, Differences in abalone growth and morphology between locations with high and low food availability: morphologically fixed or plastic traits. *Marine Biology*, 156: 1255–1263.
- SCARABINO, V., 1977, Moluscos del Golfo San Matías (Provincia de Río Negro, República Argentina), Inventario y claves para su identificación. *Comunicaciones de la Sociedad Malacológica del Uruguay*, 4(31–32): 177–297.

- SCHNACK, E., S. ALLIOTTA, F. ISLA & G. O. LIZASOAIN, 1996, Formas de fondo asociadas a un delta de reflujo macromareal, San Antonio Oeste, Provincia de Río Negro, Argentina. *Thalassas*, 12: 121–135.
- SIMONE, L. R. L., 1996, Anatomy and systematics of *Buccinanops gradatus* (Deshayes, 1844) and *Buccinanops moniliferus* (Kiener, 1834) (Neogastropoda, Muricoidea) from the southeastern coast of Brazil. *Malacologia*, 38: 87–102.
- SOKAL, R. R. & F. J. ROHLF, 1995, *Biometry*. Freeman & Co., New York, 887 pp.
- SOKOLOVA, I. M. & E. G. BOULDING, 2004, A neutral DNA marker suggests that parallel physiological adaptations to open shore and salt marsh habitats have evolved more than once within two different species of gastropods. *Marine Biology*, 145: 133–147.
- SOLÍS, M., 1998, Monitoring in Nuevo Gulf (Argentina): analysis of oceanographic data by geographic information systems (GIS), M.Sc. Thesis, 87 pp.
- TALLMARK, B., 1980, Population dynamics of *Nassarius reticulatus* (Gastropoda, Prosobranchia) in Gullmar Fjord, Sweden. *Marine Ecology*, 3: 51–62.

Revised ms. accepted 27 June 2010